



## Differences in flower colors between spiny and non-spiny Asteraceae species: A possible case of aposematism?

Simcha Lev-Yadun, Gidi Ne'eman, Tamar Keasar\*

Department of Biology & Environment, Faculty of Natural Sciences, University of Haifa–Oranim, Tivon, 36006, Israel

### ARTICLE INFO

Edited by Louis Ronse De Craene

#### Keywords:

Defense  
Evolution  
Herbivory  
Inflorescence  
Thorns

### ABSTRACT

Variation in flowering color among plant species is widely documented, but its ecological function is often unknown. Comparing phylogenetically related species that differ in ecology can help identify factors that select for flower colors. We compared the distribution of inflorescence colors of the 98 spiny versus the 189 non-spiny species of the Asteraceae in the flora of Israel, and found significant differences between the two groups. Yellow/white inflorescences dominate the non-spiny species, while pink/purple/blue flowers dominate the spiny plants. We hypothesize that the pink/purple/blue flowering of the spiny species may advertise their deterring spines to mammalian herbivores. This putative aposematic signal is particularly conspicuous in summer, when the surrounding landscape turns yellow and grazing pressure is highest. Additional potential adaptive functions for pink/purple/blue flowering in summer-blooming species include increased visibility to pollinators, and improved protection from radiation damage due to the flowers' high anthocyanin content. The pollinator attraction and radiation defense hypotheses, however, do not account for the observation that the spiny species that flower in yellow/white and in pink/purple/blue have overlapping blooming periods, as do yellow/white and pink/purple/blue flowers of non-spiny species. Phylogenetic constraints may further influence Asteraceae flowering colors, a hypothesis that is partially consistent with our data. Spine colors differ significantly from flower color in the spiny species, suggesting that spine and flower colors may have evolved in response to different selective agents. Proximately, the different colors of flowers and spines may reflect the cellular location of pigments in different cell types (anthocyanic red parenchyma versus yellow carotenized lignified hard cells).

### 1. Introduction

The evolution of flower colors is usually attributed to the function of pollinator attraction (Clegg and Durbin, 2003; Darwin, 1877; Faegri and van der Pijl, 1979), as flower colors often correlate with the visual abilities and foraging preferences of their pollinators (Fenster et al., 2004; Menzel and Shmida, 1993). Flower colors were also shown to be associated with chemical defense from herbivory (Hanley et al., 2009; Hinton, 1973; Irwin et al., 2003, 2004; Lev-Yadun, 2009a, 2016; Strauss et al., 2004; Strauss and Whittall, 2006) or from physiological stress (Strauss et al., 2004; Strauss and Whittall, 2006). However, these well-documented functions of flower colors are not necessarily the only ones. Here, we consider the possibility that floral colors also signal the presence of spines or thorns, whether on the inflorescences or on vegetative organs, and thereby contribute to the deterrence of mammalian herbivores.

Until recently, aposematic coloration, a well-known phenomenon in animals, has received very little attention in plants. Often, a brightly

colored animal (red, orange, yellow, white with black markings or combinations of these colors) is dangerous or unpalatable to predators. The conspicuous color confers a selective advantage because predators learn to associate the coloration with noxious qualities (Gittleman and Harvey, 1980; Ruxton et al., 2004). The view that colorful spines in plants, including in cacti, act as aposematic signals has developed over the last two decades (Lev-Yadun, 2001, 2016). It has been proposed that colorful spines and spine-associated coloration are cases of vegetal aposematic signals, analogous to such coloration of poisonous or otherwise dangerous animals. They were thus suggested to constitute a form of communication between plants and herbivores (e.g., Halpern et al., 2007; Lev-Yadun, 2001, 2009a, 2016; Lev-Yadun and Neeman, 2006; Ronel and Lev-Yadun, 2012; Rubino and McCarthy, 2004; Ruxton et al., 2004; Ruxton et al., 2004; Speed and Ruxton, 2005).

We analyzed the spine system of the Asteraceae in the flora of Israel as part of a broader research about spines and aposematic coloration as defenses from herbivory (e.g., Halpern et al., 2007; Lev-Yadun, 2001, 2009a, 2009b; Lev-Yadun and Ne'eman, 2006; Ronel et al., 2009, 2010;

\* Corresponding author.

E-mail addresses: [levyadun@research.haifa.ac.il](mailto:levyadun@research.haifa.ac.il) (S. Lev-Yadun), [gneeman@research.haifa.ac.il](mailto:gneeman@research.haifa.ac.il) (G. Ne'eman), [tkeasar@research.haifa.ac.il](mailto:tkeasar@research.haifa.ac.il) (T. Keasar).

Ronel and Lev-Yadun, 2012). Studies within this framework focused on: leaf variegation as a case of potential aposematic coloration (along with other defensive and physiological functions) in *Silybum marianum* (Lev-Yadun, 2015) and other thorny or spiny taxa (Lev-Yadun, 2009b); the spiny modules that defend spiny Asteraceae species in the Israeli flora and spine coloration (Ronel et al., 2009; Ronel and Lev-Yadun, 2012); and the probable common association of symmetry of spiny plant organs with aposematism (Lev-Yadun, 2011). However, the possible aposematic role of flower color in this spine-based defensive system has not been assessed so far.

The present study aims to address this knowledge gap, and to further investigate the possible involvement of aposematic coloration in anti-herbivore defense via visual signaling. We also determined whether spine and flower colors are correlated, as an indirect test of the hypothesis that coloration of spines and flowers could have evolved in response to the same selective agents. A previous analysis found that the spiny species of Asteraceae extend their blooming into the summer more than the non-spiny species (Ronel et al., 2010). We show that the spiny Asteraceae species commonly flower in pink/purple/blue while other non-spiny species of this family mostly have white/yellow flowers. Next, we address three adaptive hypotheses to explain this pattern: (1) The pink, purple and blue inflorescences are potentially aposematic towards mammalian herbivores, which probably exert heavier grazing pressure on species that grow and flower during the Mediterranean rainless and vegetation-poor summer than in spring. (2) Flowers (with their sensitive gametes) that are rich in pink/purple/blue anthocyanins are better defended from risks of UV radiation and from reactive oxygen species, which are highest in the sunny, dry and hot summer. (3) On the background of the yellowish summer landscape, pink/purple/blue flowers are better detected from afar by their major pollinators than yellow/white flowers.

## 2. Material and methods

### 2.1. Characterization of flower color and flowering season

Data on flower color for all native Asteraceae species in the Israeli flora (98 spiny and 189 non-spiny species) were compiled from Feinbrun-Dothan and Danin (1991), and were supplemented with data from The Flora of Israel Online (Danin, 2006), Feinbrun-Dothan (1978), Plitmann (1973), Plitmann et al. (1983), and Shmida and Darom (1985, 1986). Domesticated plants and species that arrived and were naturalized in Israel during the 20th century were excluded.

Color reflectance spectra, which are needed for modeling of flower and spine color perception by herbivores and pollinators (Arnold et al., 2010), are not available for the vast majority of the flowers in our database. Flower and spine colors were therefore classified as perceived by the human eye. Color-polymorphic species were scored according to the flower color of the most abundant morph. We used the following flower-color categories: white, yellow, white and yellow, pink, purple, blue, green and other (4 species). Spine color for 81 of the 98 spiny species was compiled from Ronel et al. (2009), Danin (2006) and from our field notes (Ronel and Lev-Yadun, 2012). The spine-color categories used were yellow, orange, yellow-orange, red, white, brown and purple.

We compiled data about the flowering season of all 98 native spiny and 189 non-spiny species of the Asteraceae from the analytical flora (Feinbrun-Dothan and Danin, 1991). We tabulated the flowering months for each species, and counted the species with various flower colors that flowered in each month. The presence of spines was shown to correlate with flowering season in a previous study (Ronel et al., 2010). To test whether flowering color also correlates with season, we plotted the seasonality of flowering within the spiny group (yellow/white flowers versus pink/purple/blue). We produced a similar plot for the non-spiny group. If pink/purple/blue flowers provide selective benefits mainly in summer (as protection from radiation damage or as advertisement to pollinators, hypotheses 2–3 above), a correlation

between flowering season and inflorescence color is expected to be evident. Species that flower in pink/purple/blue may bloom later in the season than species that flower in yellow/white, regardless of the presence of spines. We therefore tested for independence between flowering season and flower color within each group of species (see *Data analysis* section).

### 2.2. Testing for phylogenetic effects

Similarity in flowering color among species could reflect a phylogenetic constraint, namely a common evolutionary origin, rather than similar ecological adaptations (Arnold et al., 2009). A species-level phylogeny of the Asteraceae in our dataset, required for a formal test of this hypothesis (Felsenstein, 1985), is not yet available. We therefore addressed two questions that are more limited. First, we asked whether species within the same genus, which are phylogenetically closely related, tend to share the same inflorescence colors or spine colors. We also asked the complementary question, namely whether grouping of the species in our database according to flower color would reflect their systematic grouping into phylogenetic tribes within the Asteraceae.

To address the first question, we considered the genera that were represented by more than one species in the dataset. We calculated, separately for spiny and non-spiny genera, how many of them contained species of a single flower color. Within the spiny species, we also recorded the proportion of genera in which all species shared the same spine color. These proportions are expected to be ~1 if congeners, being closely related, resemble each other in flower and spine colors. To consider the second question, we sorted the species by inflorescence color and counted the number of tribes of the Asteraceae represented in each color group, following Panero and Funk's (2008) systematic classification. If flower colors are constrained by phylogenetic history, then species of the same color group (yellow/white or pink/purple/blue) are expected to belong to a single tribe.

### 2.3. Data analysis

We used Fisher's exact  $R \times C$  tests to compare: (a) the distribution of flower colors (8 categories) in spiny vs. non-spiny species (2 categories); (b) the distribution of flowering months (12 categories) in spiny vs. non-spiny species (2 categories); and (c) the distribution of flowering months (12 categories) in species flowering in yellow-white vs. species flowering in pink/purple/blue (2 categories), for spiny plants and for non-spiny ones. For these analyses, we tallied the number of species flowering in white/yellow and in pink/blue/purple in each month of the year, separately for spiny and for non-spiny plants. The statistical tests were implemented using the function `fisher.test` in R version 3.1.2 (R Development Core Team, 2008).

## 3. Results

### 3.1. The distribution of inflorescence and spine colors

The distribution of flower colors in spiny species and non-spiny species differs significantly. This difference reflects the much higher prevalence of pink/purple/blue flowers, and the lower prevalence of yellow/white flowers, in the spiny group as compared to the non-spiny species (Table 1, test for independence between the presence of spines and flower color,  $P = 0.0005$ ).

Non-spiny species flower earlier in the spring than do spiny species (test for independence between the presence of spines and flowering month,  $P = 0.005$ , Fig. 1). However, the distribution of flowering months does not differ significantly between species that flower in yellow/white and those that flower in pink/purple/blue within the spiny species (test for independence between flower color and flowering month,  $P = 0.70$ ). Likewise, within the non-spiny species, the distribution of flowering months in species with white-yellow

**Table 1**  
Inflorescence colors of spiny and non-spiny species in our data-set that belong to different Asteraceae tribes. The tribal affiliation of one pink non-spiny species is unknown. This species was excluded from the Table.

Tribe	Yellow	White	Yellow & white	Pink	Purple	Blue	Green	Other
<b>Spiny species</b>								
Anthemideae	0	0	0	0	0	0	0	0
Astereae	0	0	0	0	0	0	0	0
Calenduleae	0	0	0	0	0	0	0	0
Cichorieae	6	0	0	2	0	0	0	0
Cynareae	23	4	0	18	30	6	0	0
Gnaphalieae	1	0	0	0	0	0	0	0
Gundelieae	1	0	0	0	0	0	0	0
Heliantheae	1	0	0	0	0	0	2	0
Inuleae	4	0	0	0	0	0	0	0
Senecioneae	0	0	0	0	0	0	0	0
<b>Total</b>	<b>36</b>	<b>4</b>	<b>0</b>	<b>20</b>	<b>30</b>	<b>6</b>	<b>2</b>	<b>0</b>
<b>Non-spiny species</b>								
Anthemideae	26	0	24	0	0	0	0	0
Astereae	3	0	3	0	0	0	0	0
Calenduleae	4	0	0	0	0	0	0	1
Cichorieae	62	0	1	4	2	1	0	0
Cynareae	0	1	0	2	2	3	0	1
Gnaphalieae	16	3	0	0	0	0	1	1
Gundelieae	0	0	0	0	0	0	0	0
Heliantheae	1	0	1	0	0	0	0	0
Inuleae	17	0	0	0	0	0	1	1
Senecioneae	6	0	0	0	0	0	0	0
<b>Total</b>	<b>135</b>	<b>4</b>	<b>29</b>	<b>6</b>	<b>4</b>	<b>4</b>	<b>2</b>	<b>4</b>

inflorescences does not differ from species with pink/purple/blue inflorescences ( $P = 0.98$ ). Such differences would be expected if pink/purple/blue blooming mainly provide benefits during the summer months, either by protecting the flowers from solar radiation (hypothesis 2) or by increasing the plants' detectability for pollinating insects (hypothesis 3).

Unlike inflorescence colors of spiny plants (Table 1), spines are yellow or orange in most species (Fig. 2) unrelated to inflorescence colors. Inflorescence and spines had the same color in only 17 out of the 79 Asteraceae species studied for this character.

The complete data on inflorescence and spine colors and on flowering months for all species are summarized in Tables S1–S3.

### 3.2. Phylogenetic correlates of flowering color

Eight spiny genera that are represented by more than one species in our dataset are polymorphic regarding flower color (i.e., contain species that differ in their colors), while seven genera are composed of species that have the same color (monomorphic). Twelve non-spiny genera are flower color-polymorphic, while 20 are flower color-monomorphic. Eight spiny genera are polymorphic regarding spine color, whereas four genera are monomorphic concerning spine color. Thus, closely related, congeneric species varied in flowering color in 43% (20/47) of the cases, and in spine color in 67% (8/12) of the cases. The complementary question is whether species that share the same inflorescence color are phylogenetically related. Table 1 shows that species with pink/purple/blue flowers, whether spiny or not, belong to only two Asteraceae tribes (Cynareae and Cichorieae). These two tribes also account for 89 of the 98 spiny species in our database. Species that flower in yellow and in yellow/white, on the other hand, are phylogenetically more diverse, representing six tribes of spiny Asteraceae and nine tribes of non-spiny plants. Ten Asteraceae tribes contain plants with yellow/white flowering, when the combined data from spiny and non-spiny species are considered.

## 4. Discussion

Our analysis of the native Asteraceae species of Israel reveals that spiny plants have mainly pink/blue/purple inflorescences, whereas non-spiny species often have yellow/white inflorescences. To our knowledge, this study provides the first (albeit observational) evidence for the possible aposematic role of flower colors as advertisement of physical defense in plants.

Spiny plants occur in the two main ecoregions (Mediterranean and Desert), and are represented in all seven plant chorotypes of Israel (Ronel and Lev-Yadun, 2012). Thus, the similarities in their flower colors are unlikely to result from an adaptation to any single habitat or represent their phylogeographical origin. We considered three alternative, but not mutually exclusive, adaptive hypotheses explaining the differences in flower coloration and flowering season between non-spiny and spiny Asteraceae species: (1) Flower colors are aposematic signals that advertise the spiny plants' defenses to large herbivores during the dry season characterized by high grazing pressure. (2) Anthocyanin-rich pink/purple/blue flowers provide better protection to their sensitive gametes from UV radiation, photo-inhibition and photo-oxidation (e.g., Close and Beadle, 2003; Gould, 2004; Gould et al., 2002; Steyn et al., 2002; Strauss and Whittall, 2006) under the hot, dry and highly irradiative Near Eastern summer conditions. (3) Pink/purple/blue flower colors are more easily detected by pollinators than yellow/white flowers on the background of the yellowish summer landscape. A variant on this hypothesis is that late-flowering plants are selected for both spines (which defend from herbivory) and pink/purple/blue flowers (which enhance visibility to pollinators). All these alternatives are supported by the phenological differences between non-spiny species, which flower earlier in the season under more humid conditions, and their spiny relatives, which commonly flower later, towards the much drier summer (Ronel et al., 2010). However, hypotheses (2) (protection from radiation) and (3) (visibility to pollinators) also predict that species with yellow/white inflorescences will bloom earlier than species with pink/purple/blue inflorescences, both within the subset of spiny plants and within the subset of non-spiny species. This prediction is not supported by our data, neither for spiny species nor for non-spiny species (Fig. 1), lending support to the aposematic hypothesis. Nevertheless, the three hypotheses are mutually inclusive, thus the color differences between spiny and non-spiny plants may result from multiple selection agents, i.e., pollination, physiology, and defense from herbivory.

We also examined a non-adaptive hypothesis for the color differences between spiny and non-spiny species, namely that they reflect common evolutionary ancestry. About 60% of the genera in the present study contained species that vary in flowering color. Pink/purple/blue flowers were restricted to two tribes within the Asteraceae, while white/yellow flowers occurred in ten different tribes. Hence, phylogeny may play a role in explaining flowering color (potentially reducing the role of aposematism), but this role is likely to be partial. In particular, it seems that pink/purple/blue flowering is under a stronger phylogenetic constraint than white/yellow flowering.

What sort of defenses might the showy pink/purple/blue flowers advertise? The hypothesis that many flowers that have conspicuous colors are also toxic, and therefore their flower colors have a warning function, was one of the earliest proposals for aposematism in plants (Hinton, 1973). Fineblum and Rausher (1997) proposed that since anthocyanin-based flower color and defensive molecules have common biochemical pathways, this may defend flowers from herbivory. Schaefer and Rolshausen (2006) suggested that herbivorous insects will feed less on plants that have strong anthocyanin coloration because it correlates with the strength of a chemical defense. Rothschild (1986), and later Lev-Yadun (2006, 2009a, 2016) and Lev-Yadun and Gould (2007, 2009), proposed that the association of conspicuous coloration with defensive chemicals should be considered aposematic. These hypotheses are supported by numerous case-studies, where anthocyanins

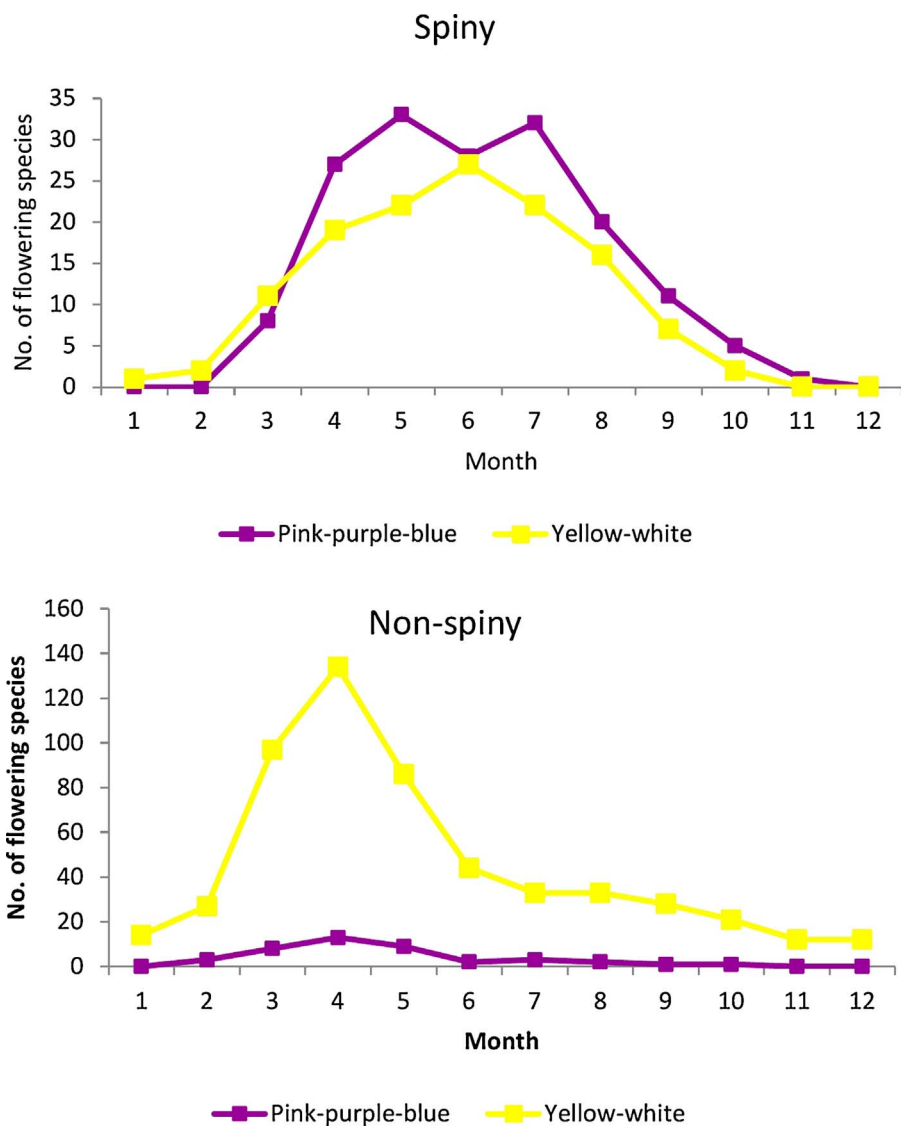


Fig. 1. Distribution of flowering months for spiny (n = 98) and non-spiny (n = 189) pink-purple-blue and yellow-white Asteraceae species in Israel. Since most species flower over more than one month, the total number of counts plotted (the area under the curves) is higher than the number of species analyzed.

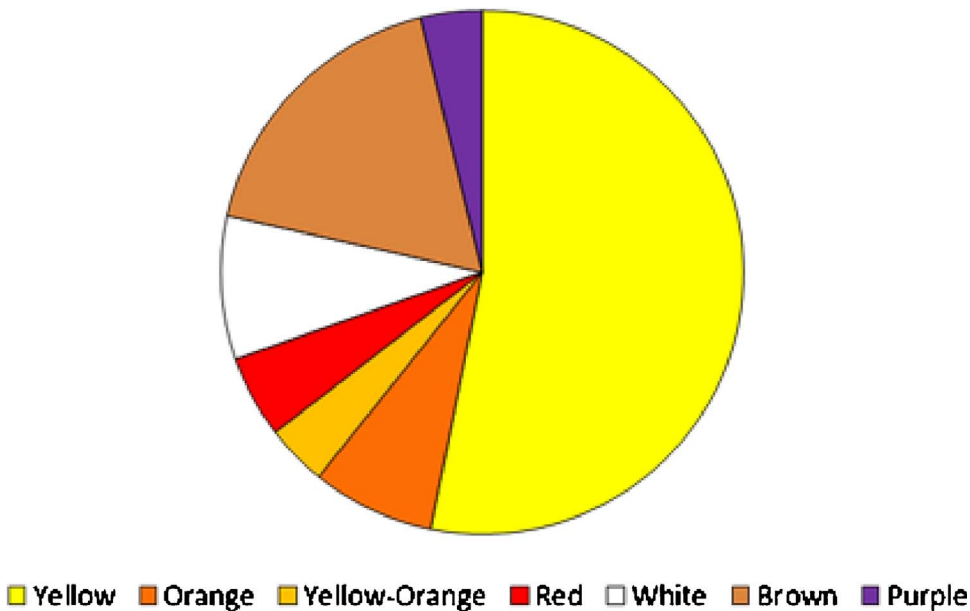


Fig. 2. Distribution of spine colors in Asteraceae species in Israel (n = 81).



are associated with defensive chemicals that reduce herbivory (e.g., Archetti, 2009; Cooney et al., 2012; Gerchman et al., 2012; Irwin et al., 2003, 2004; Lev-Yadun, 2016; Maskato et al., 2014).

The possibility that flowers may be both conspicuous and spiny, thus aposematically advertising their physical defense mechanisms, was first considered less than a decade ago (Lev-Yadun, 2009a, 2011, 2016; Ronel and Lev-Yadun, 2012; Ronel et al., 2009). Flower color can potentially enhance the visual signals of the spines themselves, thus making aversive learning by herbivores quicker and stronger. This would be similar to the increased effect of multiple plant signals (e.g. color and odor) in attracting pollinators (Leonard et al., 2011). Aposematism in spiny inflorescences of the Asteraceae may be manifested through conspicuous colors of their flowers, of their surrounding spines, or both (Lev-Yadun, 2011). Interestingly, we found that inflorescence and spine colors differed in most species. Possibly, the evolution of flower and spine coloration is driven by different selective agents, such as pollinators, insect and mammalian herbivores. Mechanistically, the different coloration of flowers and spines may be due to differences in pigment chemistry and in the type of cells and sub-cellular organelles associated with the pigments. Colorful turgid pink, red, purple and blue flowers contain hydrophilic anthocyanins in large vacuoles, whereas dry and hard spines owe their common yellow pigmentation to hydrophobic membrane-bound carotenoids in chromoplasts (Lee, 2007).

Although a confident classification of an organism as exhibiting aposematic signaling requires experiments that demonstrate associative learning in its predator/herbivore, this has been shown for only a tiny fraction of the animal species classified as aposematic. Direct experimental data concerning spiny plants is even scarcer (Lev-Yadun, 2009a, 2016; Schaefer and Ruxton, 2011). In contrast, some good experimental data about visual aposematism of toxic plants exists (Archetti, 2009; Cooney et al., 2012; Maskato et al., 2014). While it clearly indicates that this defensive strategy indeed operates in plants, much more experimentation is needed, especially under field conditions (Lev-Yadun, 2016; Schaefer and Ruxton, 2011). Observations of the foraging behavior of naïve vs. experienced herbivores, on spiny plants with bluish vs. yellowish inflorescences, are a first and necessary step. These should be followed by controlled comparisons of herbivory levels on different flower-color morphs of the same spiny species. Experiments involving spine removal, and manipulations of inflorescence and spine colors, will allow testing of the relative effects of the plants' spines and the associated color signals on grazers. Datasets of spiny and non-spiny species from other regions of the world should also be analyzed for flower colors. Parallel studies should determine and consider the role of phylogeny in our data-set, inflorescence and spine color-reflectance spectra and their perception by their main herbivores. In combination, these proposed tests will allow a critical evaluation of our hypothesis.

## Acknowledgements

We thank several anonymous referees for helpful comments on earlier versions of the manuscript. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.flora.2017.12.002>.

## References

Archetti, M., 2009. Evidence from the domestication of apple for the maintenance of autumn colours by coevolution. *Proc. R. Soc. B* 276, 2575–2580.  
 Arnold, S.E.J., Le Comber, S.C., Chittka, L., 2009. Flower color phenology in European grassland and woodland habitats: through the eyes of pollinators. *Isr. J. Plant Sci.* 57,

211–230.  
 Arnold, S.E.J., Faruq, S., Savolainen, V., McOwan, P.W., Chittka, L., 2010. FRD: the floral reflectance database—a web portal for analyses of flower colour. *PLoS One* 5, e14287.  
 Clegg, M.T., Durbin, M.L., 2003. Tracing floral adaptations from ecology to molecules. *Nat. Rev. Genet.* 4, 206–215.  
 Close, D.C., Beadle, C.L., 2003. The ecophysiology of foliar anthocyanin. *Bot. Rev.* 69, 149–161.  
 Cooney, L.J., van Klink, J.W., Hughes, N.M., Perry, N.B., Schaefer, H.M., Menzies, I.J., Gould, K.S., 2012. Red leaf margins indicate increased polygodial content and function as visual signals to reduce herbivory in *Pseudowintera colorata*. *New Phytol.* 194, 488–497.  
 Danin, A. (Ed.), 2006. Flora of Israel Online. The Hebrew University of Jerusalem, Israel and continuously updated. <http://flora.org.il/en/plants>.  
 Darwin, C., 1877. *The Different Forms of Flowers on Plants of the Same Species*. John Murray, London.  
 Faegri, K., van der Pijl, L., 1979. *The Principles of Pollination Ecology*, 3rd ed. Pergamon Press, Oxford.  
 Feinbrun-Dothan, N., Danin, A., 1991. *Analytical Flora of Eretz-Israel*. Cana, Jerusalem (Hebrew).  
 Feinbrun-Dothan, N., 1978. *Flora Palaestina*, vol. III The Israel Academy of Sciences and Humanities, Jerusalem.  
 Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.  
 Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Evol. Syst.* 35, 375–403.  
 Fineblum, W.L., Rauscher, M.D., 1997. Do floral pigmentation genes also influence resistance to enemies? The W locus in *Ipomoea purpurea*. *Ecology* 78, 1646–1654.  
 Gerchman, Y., Dodek, I., Petichov, R., Yerushalmi, Y., Lerner, A., Keasar, T., 2012. Beyond pollinator attraction: extra-floral displays deter herbivores in a Mediterranean annual plant. *Evol. Ecol.* 26, 499–512.  
 Gittleman, J.L., Harvey, P.H., 1980. Why are distasteful prey not cryptic? *Nature* 286, 149–150.  
 Gould, K.S., Neill, S.O., Vogelmann, T.C., 2002. A unified explanation for anthocyanins in leaves? *Adv. Bot. Res.* 37, 167–192.  
 Gould, K.S., 2004. Nature's Swiss army knife: the diverse protective roles of anthocyanins in leaves. *J. Biomed. Biotechnol.* 5, 314–320.  
 Halpern, M., Raats, D., Lev-Yadun, S., 2007. Plant biological warfare: thorns inject pathogenic bacteria into herbivores. *Environ. Microbiol.* 9, 84–592.  
 Hanley, M.E., Lamont, B.B., Armbruster, W.S., 2009. Pollination and plant defense traits co-vary in Western Australian *Hakeas*. *New Phytol.* 182, 251–260.  
 Hinton, H.E., 1973. Natural deception. In: Gregory, R.L., Gombich, E.H. (Eds.), *Illusion in Nature and Art*. Duckworth, London, pp. 97–159.  
 Irwin, R.E., Strauss, S.Y., Storz, S., Emerson, A., Guibert, G., 2003. The role of herbivores in the maintenance of a flower color polymorphism in wild radish. *Ecology* 84, 1733–1743.  
 Irwin, R.E., Adler, L.S., Brody, A.K., 2004. The dual role of floral traits: pollinator attraction and plant defense. *Ecology* 85, 1503–1511.  
 Lee, D., 2007. *Nature's Palette, the Science of Plant Color*. University of Chicago Press, Chicago.  
 Leonard, A.S., Dornhaus, A., Papaj, D.R., 2011. Flowers help bees cope with uncertainty: signal detection and the function of floral complexity. *J. Exp. Biol.* 214, 113–121.  
 Lev-Yadun, S., Gould, K.S., 2007. What do red and yellow autumn leaves signal? *Bot. Rev.* 73, 279–289.  
 Lev-Yadun, S., Gould, K.S., 2009. Role of anthocyanins in plant defense. In: Gould, K.S., Davies, K.M., Winefield, C. (Eds.), *Life's Colorful Solutions: The Biosynthesis, Functions, and Applications of Anthocyanins*. Springer-Verlag, Berlin, pp. 21–48.  
 Lev-Yadun, S., Ne'eman, G., 2006. Color changes in old aposematic thorns, spines, and prickles. *Isr. J. Plant Sci.* 54, 327–333.  
 Lev-Yadun, S., 2001. Aposematic (warning) coloration associated with thorns in higher plants. *J. Theor. Biol.* 210, 385–388.  
 Lev-Yadun, S., 2006. Defensive coloration in plants: a review of current ideas about anti-herbivore coloration strategies. In: Teixeira da Silva, J.A. (Ed.), *Floriculture, Ornamental and Plant Biotechnology: Advances and Topical Issues*, vol. IV. Global Science Books, London, pp. 292–299.  
 Lev-Yadun, S., 2009a. Aposematic (warning) coloration in plants. In: Baluska, F. (Ed.), *Plant-Environment Interactions, from Sensory Plant Biology to Active Plant Behavior*. Springer Verlag, Berlin, pp. 167–202.  
 Lev-Yadun, S., 2009b. Müllerian and Batesian mimicry rings of white-variegated aposematic spiny and thorny plants: a hypothesis. *Isr. J. Plant Sci.* 57, 107–116.  
 Lev-Yadun, S., 2011. Fearful symmetry in aposematic plants. *Plant Signal. Behav.* 6, 1739–1740.  
 Lev-Yadun, S., 2015. The proposed anti-herbivory roles of white leaf variegation. *Prog. Bot.* 76, 241–269.  
 Lev-Yadun, S., 2016. *Defensive (Anti-Herbivory) Coloration in Land Plants. Anti-Herbivory Plant Coloration and Morphology*. Springer, Zug.  
 Maskato, Y., Talal, S., Keasar, T., Gefen, E., 2014. Red foliage color reliably indicates low host quality and increased metabolic load for development of an herbivorous insect. *Arthropod-Plant Interact.* 8, 285–292.  
 Menzel, R., Shmida, A., 1993. The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case. *Biol. Rev.* 68, 81–120.  
 Panero, J.L., Funk, V.A., 2008. The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Mol. Phylogenet. Evol.* 47, 757–782.  
 Plitmann, U., Heyn, C., Danin, A., Schmida, A., 1983. *Pictorial Flora of Israel*. Massada, Givatayim.  
 Plitmann, U., 1973. Taxonomic studies in *Centaurea* sect. *Calcitrapa*. I. New taxa in

- Palestine. *Isr. J. Bot.* 22, 47–66.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Ronel, M., Lev-Yadun, S., 2012. The spiny, thorny and prickly plants in the flora of Israel. *Bot. J. Linn. Soc.* 168, 344–352.
- Ronel, M., Khateeb, S., Lev-Yadun, S., 2009. Protective spiny modules in thistles of the Asteraceae in Israel. *J. Torrey Bot. Soc.* 136, 46–56.
- Ronel, M., Ne'eman, G., Lev-Yadun, S., 2010. Spiny east-Mediterranean plant species flower later and in a drier season than non-spiny species. *Flora* 205, 276–281.
- Rothschild, M., 1986. The red smell of danger. *New Sci.* 111, 34–36.
- Ruxton, G.D., Sherratt, T.N., Speed, M.P., 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford.
- Schaefer, H.M., Rolshausen, G., 2006. Plants on red alert: do insects pay attention? *BioEssays* 28, 65–71.
- Schaefer, H.M., Ruxton, G.D., 2011. *Plant-Animal Communication*. Oxford University Press, New York.
- Shmida, A., Darom, D., 1985. *Handbook of Wildflowers of Israel. Mediterranean Flora*. Keter (in Hebrew), Jerusalem.
- Shmida, A., Darom, D., 1986. *Handbook of Wildflowers of Israel. Desert Flora*. Keter (in Hebrew), Jerusalem.
- Speed, M.P., Ruxton, G.D., 2005. Warning displays in spiny animals: one (more) evolutionary route to aposematism. *Evolution* 59, 2499–2508.
- Steyn, W.J., Wand, S.J.E., Holcroft, D.M., Jacobs, G., 2002. Anthocyanins in vegetative tissues: a proposed unified function in photoprotection. *New Phytol.* 155, 349–361.
- Strauss, S.Y., Whittall, J.B., 2006. Non-pollinator agents of selection on floral traits. In: Harder, L.D., Barrett, S.C.H. (Eds.), *The Ecology and Evolution of Flowers*. Oxford University Press, Oxford, pp. 120–138.
- Strauss, S.Y., Irwin, R.E., Lambrix, V.M., 2004. Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. *J. Ecol.* 92, 132–141.